Vol. 110. Part 17*. Pp. 533–566. 1 fig. 2 plates. 31st December, 1958.

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World List abbreviation: *Trans. R. ent. Soc. Lond.*

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GENERAL INDEX, VOL. 110 555–566

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 14s. 0d.

* With Title page, Contents and Index.

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OBSERVATIONS ON THE BIOLOGY OF *CARAPHRACTUS CINCTUS* WALKER (HYMENOPTERA: MYMARIDAE), A PARASITOID OF THE EGGS OF DYTISCIDAE.

I. Methods of Rearing and Numbers Bred on Different Host Eggs

By Dorothy J. Jackson

Manuscript received 29th March, 1958

(Read 7th May, 1958)

With 2 Plates and 1 Text-figure

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I. Introduction

The Fairy Fly *Caraphractus cinctus* Walker, known formerly as *Polynema natans* Lubbock, has attracted the attention of entomologists for many years, on account of its remarkable capacity for swimming submerged in the water by rapid vibrations of its wings. In 1954, I found it to be a common parasitoid of the eggs of Dytiscidae in Fife (Jackson, 1954), and the next summer I commenced to breed the insect, but many difficulties were encountered in obtaining Dytiscid eggs laid under reliable conditions for rearing the parasite, and a method had to be devised to provide a succession of host eggs of different species from early spring to late autumn. This has now been achieved and the first part of this paper is concerned with the breeding technique.

I have now been breeding this Mymarid in numbers for three years, and its biology presents many interesting features. It provides excellent material for the study of sex ratio in large and in small host eggs, for in the eggs of *Dytiscus marginalis* parasitised by a single mated female, the proportion of female offspring reared is greatly in excess of that resulting when a mated female lays in a few eggs of *Agabus*.

It was observed in 1955 that the size of individuals bred from *Agabus* eggs was very variable, depending on the number of individuals present in an egg, and that when five or more developed in one egg, some or all were small and brachypterous. Preliminary breeding experiments had shown that when a macropterous female lays several eggs in a small host egg, some at least of the progeny are small and have reduced wings, and conversely when a brachypterous female lays one or two eggs in one host egg the progeny are of normal size and macropterous (Jackson, 1955). Since then, as a result of breeding the species on a variety of host eggs, it has been found that the problem is more complicated, for the production of brachypterous specimens does not occur in all overcrowded eggs (pp. 536 and 547).

I experienced much difficulty in getting eggs superparasitised owing to the remarkable discrimination and restraint in oviposition shown by the female *Caraphractus*. Before laying she probes each egg with her ovipositor, but, if the egg is already parasitised, in most cases she withdraws her ovipositor in from 10 to 30 seconds without laying. In a normal oviposition the ovipositor is held in the egg usually from one and a half to three minutes (fig. 1) and, after withdrawing it, the female walks back and forwards over the egg and cleans herself; but after an exploratory thrust into an already parasitised egg the female leaves the egg abruptly and looks for another. As far as I am aware such discrimination and restraint in laying, though well known in other parasitic Hymenoptera, has not been recorded before in the Mymaridae, nor for an insect laying its eggs under water. I have made many observations on this behaviour of the female, combined with experiments on exposing eggs already laid in by an unmated female to a mated female, and rearing the offspring. If females result, it is certain that a second laying has occurred, for unmated females of *Caraphractus* produce only males. A full account of these experiments and of the process of oviposition will be given in a subsequent paper.

Once the problem of obtaining host eggs had been solved, *Caraphractus cinctus* proved an easy insect to breed. The females are very prolific and are usually ready to oviposit directly an egg is offered. Moreover the host eggs I have mostly used (those of certain *Agabus*, *Ilybius* and *Dytiscus*) have transparent shells so that the development of the parasites can be watched once the larvae are half grown. This allows of isolating the host eggs before the imagines are ready to emerge. No detailed work appears to have been published on the biology of an aquatic Hymenopteron, and, since the problems encountered are similar to those found in parasitoids of other groups, it is hoped that this investigation will be of interest to other workers.

Acknowledgments

I am greatly indebted to Dr. George Salt, F.R.S., for the valuable help he has given me in so kindly reading over and commenting on the typescript of this paper, and I have also appreciated his helpful advice on various occasions. I am most grateful to Dr. W. D. Hincks for his initial help in identifying the species and for his continued interest in my work. Professor H. G. Callan of St. Andrews University, and Mr. R. Mere have kindly provided me with living specimens of *Dytiscus marginalis* which have proved most useful, and Mr. A. E. Gardner has very kindly sent me eggs of Odonata.

The photographs of the imagines of *Caraphractus* were taken by Mr. E. A. Carstairs of the Physiology Department, St. Andrews University (with kind permission of Dr. G. R. Tristram), and I am grateful to him for his skilled work. Mr. D. R. R. Burt of the Natural History Department, St. Andrews University, kindly took the photograph forming Plate IIA, and I am indebted to Mr. W. H. T. Tams of the British Museum (Natural History) for his fine photograph of pupae of *Caraphractus* in *Dytiscus* eggs. I am most grateful to the staff of the University Library, St. Andrews, for the trouble they have taken to procure various books for me, and also to Miss Evans of the Royal Entomological Society of London for similar help.

II. Historical Notes with Comments

Walker described this species in 1846 as *Caraphractus cinctus*. It was found by Haliday on long grass in drains. Later, in 1864, the species was found by Lubbock and named by him *Polynema natans*. He gives an interesting account of the habits of the imagines in both this species and *Prestwichia aquatica* Lubbock. He draws attention to the fact that, though both species are essentially aquatic in their habits, neither shows any structural adaptations for life under water, and, though the wings of *Polynema* so closely resemble those of *Prestwichia*, the former swims " only with its wings and the other with its legs ". Walker (1873) pointed out that, according to Haliday, Lubbock's *Polynema natans* was *Caraphractus cinctus* Hal. Westwood (1879) placed the species in the genus *Anaphes*, and the name *Anaphes cinctus* Hal. is used by Blunck (1914) and Rimsky-Korsakov (1916) but, later, the name *Caraphractus cinctus* Walker appears to be generally adopted. Henriksen (1919) gives a useful chronological list of references to this species up to 1917.

Apart from the confusion in the nomenclature of this insect, a mistake in regard to its biology was made by Ganin (1869). He described a species of *Polynema* as having been bred from the eggs of *Agrion* (*Calopteryx*) *virgo*. The figures given by him of a " histriobdellid " larva certainly do not refer to the larva of *Caraphractus*, and Brocher (1910), Thienemann (1916) and Henriksen (1922) show that the species Ganin observed must belong to the genus *Anagrus*. Moreover Henriksen states that *Anagrus subfuscus* Forst. was recorded by Heymons from eggs of *Agrion* (*Calopteryx*) *virgo*. Rimsky-Korsakov (1916, 1925) arrived at the same conclusion, and he had bred *Anagrus subfuscus* from the eggs of *Agrion* and *Lestes* (1916).

The statement that *Caraphractus cinctus* is a parasite of the eggs of dragonflies has unfortunately been repeated in many books on aquatic insects, *e.g.* by Miall (1912), Wesenberg-Lund (1943 : 580) and more recently by Bertrand (1954). Whether their statements have any basis in fact seems very doubtful in view of my complete failure to interest the female *Caraphractus* in eggs of certain Odonata, as will be described later (p. 542).

Caraphractus cinctus has been recorded in America, from Ithaca, by Matheson and Crosby (1912), from the eggs of *Notonecta* in stems of aquatic plants. I have made repeated attempts to get *Caraphractus* to parasitise eggs of *Notonecta* but without success. Grant (1931–32) refers to *Polynema natans* as parasitising the eggs of pond skaters but this record requires confirmation.

Rimsky-Korsakov (1925), in his important paper on the biology of *Cara-*

phractus cinctus, records the rearing of this species from eggs of *Dytiscus*, *Ilybius* and smaller Dytiscidae—the species not specified. In this paper he describes a brachypterous *Caraphractus* as a new species, *C. reductus*, both male and female, although Nikol'shaya (1952) states erroneously that only the male of *C. reductus* Rim.-Kor. is known. During the course of over 300 breeding experiments I have frequently obtained specimens of *C. cinctus* with short wings, bred from macropterous parents and vice versa (Plate Ia and b). These short-winged specimens closely resemble the description and figures of *C. reductus* Rim.-Kor. given by Rimsky-Korsakov, but they are merely small brachypterous specimens of *C. cinctus*. Specimens of all wing sizes have been obtained in my experiments, and the smaller specimens are frequently, but not invariably, short-winged. Such brachypterous specimens occur most frequently in superparasitised eggs (p. 547), especially those of *Agabus sturmii*, so I see no reason to consider that two species are involved, and I believe that *C. reductus* is merely a dwarfed form of *C. cinctus*. Before starting breeding experiments I forwarded some brachypterous specimens, bred from collected host eggs, to Dr. W. D. Hincks. He considered them to be brachypterous *Caraphractus cinctus* and his view has been fully confirmed by the breeding experiments.

III. Distribution of *Caraphractus cinctus* in Britain

As far as I know the only record of breeding *Caraphractus cinctus* in this country is the brief reference by Burgess-Sopp (1905) to its parasitism of the egg of *Dytiscus semisulcatus* Müll. (*punctulatus* F.). Several records exist of the capture of the imagines of this Mymarid in various parts of England—at Oxford by Hamm (1917) on different dates from 22nd September to 27th October, 1917; at Chiselhurst by Sir John Lubbock (Lord Avebury) in 1863 (Burton 1895); at Totterbridge by Burton (1895); while Britten took it at Levenshulme, Manchester in 1918 (Britten, 1919). I have found it to be common in small sheltered pools and ponds in Fife (Jackson, 1956), where a variety of Dytiscidae occurred and where there was plenty of vegetation for the beetles to lay on. A sequence of eggs of a few common Dytiscidae are essential to the breeding of this Mymarid, though the fact that some individuals of all generations may go into diapause in the prepupal state within the host egg will assist in the survival of the parasite when suitable hosts are scarce.

IV. Technique and Methods of Rearing

I first obtained this parasite from the eggs of *Dytiscus* and also from the much smaller egg of an *Agabus*, identified later as *A. sturmii* Gyllenhal. Since the eggs of *Dytiscus marginalis* are only to be found in the spring and early summer, and since no overwintering stage of the parasite has been found in *Dytiscus* eggs, it is evident that it must utilise the eggs of other water beetles in order to continue breeding throughout the summer. For this reason observations were made on the egg-laying habits of various Dytiscidae, including *Colymbetes fuscus* L., *Ilybius fuliginosus* F., *I. ater* Degeer, *Hydroporus planus* F. and various species of *Agabus*, and observations on oviposition in the genus *Agabus* have been recorded (Jackson, 1958*b*).

It was necessary to know how and where the various species laid their eggs and also the months during which oviposition occurred. Not all the eggs obtained

proved suitable hosts for *Caraphractus*, since there was a very high mortality of the parasite in eggs of *Colymbetes fuscus* and *Agabus chalconatus*, while the small eggs of *Hydroporus planus* were usually ignored by the female parasites.

The most important requirement for experimental breeding was to obtain eggs of water beetles laid under conditions excluding the possibility of previous parasitism. It was never safe to place the beetles with plants uprooted from a pond, as these might already contain parasitised beetle eggs hidden in their tissues. Similarly, when feeding captive beetles, it was necessary to wash thoroughly each *Chironomus* or other larva offered, as if larvae in pond water were supplied, females of *Caraphractus* might already be present in the water. It was found latterly that aquatic worms, sold by aquarists as " Tubifex ", were a suitable food for the beetles. These were received in a solid mass and lived for months in a basin of water under a dripping tap.

(1) *Obtaining the Host Eggs*

Since the eggs of the various water beetles are laid in different ways (depending largely on whether or not the beetle is provided with a cutting ovipositor), it is convenient to consider the species separately, and to describe the methods employed to obtain eggs suitable for experimental breeding of the parasite.

Dytiscus marginalis L.

As is well known, this species is provided with a cutting ovipositor and embeds its eggs in the tissues of the leaves or stalks of various water plants. I have frequently found the eggs laid within the sheathing leaves of *Juncus articulatus* L. growing submerged in water (Plate IIA). This plant grows equally well in damp fields. In the autumn of 1955 and 1956 I therefore uprooted some plants growing in a grassy area where no water lay and planted them in garden soil in large jars or tanks of water. They grew well, submerged in the water, and by spring they were available for the females for oviposition. To supplement these plants, I supplied the beetles with cut shoots of *Eriophorum*, *Phragmites* and *Carex otrubae* Podh (*vulpina* L.) (collected where growing out of water), or with the cut blades of such tall grasses as *Arrhenatherum*, *Phalaris* or *Dactylis glomerata* L., while the leaves of *Luzula sylvatica* Gaud. were readily accepted. Such plants were plunged in the water of the jars with the cut stalks so secured that they stood upright ; but it was found that the beetles also laid on leaves floating on the surface. In the leaves of all these plants the beetles laid readily, the eggs being placed between the upper and lower epidermis, but there was a good deal of mortality amongst the unparasitised eggs of this beetle. This mortality proved a troublesome factor in certain breeding experiments with the Mymarid, which only develops on healthy, fertile eggs. The cause of this mortality is unknown, but in some cases it was probably due to the leaves of non-aquatic plants proving too stiff to allow of the normal increase in size of the egg during development, and Joly (1945) notes that eggs laid on a plant with a hard envelope, like the stalk of *Carex*, developed no further. He found the yield to be almost 100 per cent. in plants with tender stalks, such as *Potamogeton* or *Caltha*. I have found that *Caltha* is not a suitable plant to use in rearing *Caraphractus*, for cut pieces of stems containing *Dytiscus* eggs soon become putrid in tubes of water. The leaves of *Carex otrubae* proved excellent, keeping

sufficiently fresh in water for the development of the parasite. *Luzula* leaves proved the best of the non-aquatic plants, as the leaves appeared to be of the right consistency and eggs laid in them usually developed. Eggs laid in withered grass leaves sometimes remained healthy, though Blunck (1914 : 101) states that living plant tissue is necessary for development of the egg of *Dytiscus*. Eggs which the females dropped instead of inserting in the leaf never developed and became mouldy, and Joly suggests that such eggs are virgin and that the fertilisation of the egg is affected as the result of a reflex initiated by the pushing of the ovipositor into the stalk of a plant. *Caraphractus* females were never seen to oviposit in these dropped eggs ; they sometimes prick infertile eggs with the ovipositor but reject them, so that they must be able to discriminate between fertile and infertile eggs.

The eggs of *Dytiscus marginalis* L.[1] were obtained from several females each kept alone, usually in a 12-inch glass jar, in an unheated north room. The eggs were laid from early March to mid-June—a few as late as mid-July. This corresponds with the finding of eggs in ponds in Fife from mid-March to mid-June.

It was found that only about half the females obtained in Fife in May, 1956, were laying that season. Those that did not lay were kept outside throughout the winter in a large barrel covered with a close-meshed wire lid which prevented their escape. The following spring these beetles started laying and their eggs were fertile, though the females had been isolated from males for a year. Blunck (1913) states that the beetles on emergence possess quite undeveloped ovaries and that oviposition of the six-month-old beetles and those 18 months old takes place at the same time in spring, so that in May, 1956, there is little doubt that the beetles that failed to lay were sexually immature. The beetles were fed principally on small earthworms, and on tadpoles when these were available ; the latter were washed before placing them with the beetles.

The size of newly-laid *Dytiscus* eggs given by Blunck (1914) is 6·5–7·5 by 1·2 mm. Those I have measured were 6·8–7·1 by 1·4 mm. Eggs containing parasites of *Caraphractus cinctus* may measure up to 8·2 mm. in length. The shell of the egg will stretch under pressure of the growing parasite larvae just as happens in the normal development of the egg. The incubation period in an unheated north room was about three weeks. Blunck (1914) found that eggs laid in early spring required from four to six weeks or longer for development, but for eggs laid later in the season the period of development was reduced to 14 days.

Ilybius fuliginosus F.

This beetle is provided with a saw-like ovipositor and places her eggs in holes which she cuts in the leaf tissue. As a consequence, a triangular tongue of leaf tissue is left projecting above the scar and is a help in finding the eggs. Eggs were first found in great numbers on the leaf stalks of *Alisma plantago-aquatica* L., but, as this plant could not be maintained under conditions exclud-

[1] All the *Dytiscus* eggs mentioned in this paper are those of *D. marginalis*. Unfortunately it was not possible to obtain *D. semisulcatus* Müller, in which, according to Joly (1945), the laying period is longer, occurring in spring and autumn and sometimes in the winter.

ing all possibility of previous infection by the parasite, *Juncus articulatus* was used in the breeding experiments with *Caraphractus* according to the method described above. The eggs of *I. fuliginosus* are deposited in the hollow air-filled leaves of the *Juncus* and are completely hidden from view, but the scar with the tongue-like projection shows, and, if a leaf is held up to the light it will be seen to be riddled with holes. By ripping up the leaf the eggs are revealed lying lengthwise, often several in one leaf with intervals between them. It is the slender floating leaves of the *Juncus*, about one-eighth inch in diameter, that are principally selected by the female. I have also found the eggs of this species commonly in the still finer leaves of *Juncus bulbosus* L., only 1 mm. in diameter. I tried the female beetles with cut leaves of *J. articulatus*, not grown in water ; scars were made on the leaves but, while one egg was found outside the leaf, none occurred inside and I think the leaves are too tough for normal oviposition unless grown in water.

The eggs are laid mainly from the end of June until the beginning of August and they have proved invaluable for maintaining the summer generations of *Caraphractus cinctus*, as few *Agabus* and no *Dytiscus marginalis* eggs are normally available at this time. The eggs measure, when recently laid, 1·3 by 0·5 mm. and they increase in size to 1·5 by 0·7 mm. as the larva develops. It is a more elongated egg than that of *Agabus bipustulatus*, and differently shaped, being more curved on the dorsal than on the ventral side. One *fuliginosus* egg kept under observation hatched in about 16 days.

Ilybius ater Degeer

The laying habits of this species are closely similar to those of *I. fuliginosus*, but the eggs are much larger, 1·8–1·9 by 0·9 mm. I have had a female laying from the beginning of June to August.

Colymbetes fuscus L.

My observations are limited to two specimens which laid during April and May. The eggs are affixed with a cement covering on to the surface of the leaves of various aquatic plants, such as *Myosotis* or *Elodea*, and they were also laid on grass leaves placed in the water. The eggs are pale yellow when first laid but become greyish-brown in a few days. The beetles fed readily on earthworms and *Chironomus*, but seemed unable to deal with tadpoles. Two newly-laid eggs measured 1·7 by 0·8 mm. The incubation period was under 12 days.

Hydroporus planus F.

As I wished to get some very small eggs for an experiment designed to obtain brachypterous *Caraphractus*, I collected some specimens of *H. planus* in early March, 1956. They laid eggs close to the axil of the leaves of *Elodea*, mostly on faded leaves near the base of the shoot. Each egg is surrounded with a voluminous gelatinous mass which sticks it to the leaf. The beetles also laid on sphagnum moss and on a feathery moss collected from dry ground, and these eggs were safe to use in my breeding experiments. Only in one instance was successful parasitism obtained with an egg of *H. planus*. The egg, measuring 0·68 by 0·41 mm., was parasitised by an unmated macropterous female and a single male with rather short wings was duly reared from it.

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ing all possibility of previous infection by the parasite, *Juncus articulatus* was used in the breeding experiments with *Caraphractus* according to the method described above. The eggs of *I. fuliginosus* are deposited in the hollow air-filled leaves of the *Juncus* and are completely hidden from view, but the scar with the tongue-like projection shows, and, if a leaf is held up to the light it will be seen to be riddled with holes. By ripping up the leaf the eggs are revealed lying lengthwise, often several in one leaf with intervals between them. It is the slender floating leaves of the *Juncus*, about one-eighth inch in diameter, that are principally selected by the female. I have also found the eggs of this species commonly in the still finer leaves of *Juncus bulbosus* L., only 1 mm. in diameter. I tried the female beetles with cut leaves of *J. articulatus*, not grown in water ; scars were made on the leaves but, while one egg was found outside the leaf, none occurred inside and I think the leaves are too tough for normal oviposition unless grown in water.

The eggs are laid mainly from the end of June until the beginning of August and they have proved invaluable for maintaining the summer generations of *Caraphractus cinctus*, as few *Agabus* and no *Dytiscus marginalis* eggs are normally available at this time. The eggs measure, when recently laid, 1·3 by 0·5 mm. and they increase in size to 1·5 by 0·7 mm. as the larva develops. It is a more elongated egg than that of *Agabus bipustulatus*, and differently shaped, being more curved on the dorsal than on the ventral side. One *fuliginosus* egg kept under observation hatched in about 16 days.

Ilybius ater Degeer

The laying habits of this species are closely similar to those of *I. fuliginosus*, but the eggs are much larger, 1·8–1·9 by 0·9 mm. I have had a female laying from the beginning of June to August.

Colymbetes fuscus L.

My observations are limited to two specimens which laid during April and May. The eggs are affixed with a cement covering on to the surface of the leaves of various aquatic plants, such as *Myosotis* or *Elodea*, and they were also laid on grass leaves placed in the water. The eggs are pale yellow when first laid but become greyish-brown in a few days. The beetles fed readily on earthworms and *Chironomus*, but seemed unable to deal with tadpoles. Two newly-laid eggs measured 1·7 by 0·8 mm. The incubation period was under 12 days.

Hydroporus planus F.

As I wished to get some very small eggs for an experiment designed to obtain brachypterous *Caraphractus*, I collected some specimens of *H. planus* in early March, 1956. They laid eggs close to the axil of the leaves of *Elodea*, mostly on faded leaves near the base of the shoot. Each egg is surrounded with a voluminous gelatinous mass which sticks it to the leaf. The beetles also laid on sphagnum moss and on a feathery moss collected from dry ground, and these eggs were safe to use in my breeding experiments. Only in one instance was successful parasitism obtained with an egg of *H. planus*. The egg, measuring 0·68 by 0·41 mm., was parasitised by an unmated macropterous female and a single male with rather short wings was duly reared from it.

(2) *Conducting the Breeding Experiments*

The eggs to be parasitised were kept in glass dishes of water with one or more ovipositing females of *Caraphractus* ; observations on laying were made with a binocular microscope in a strong light which did not in any way interfere with the activities of the female. Once the female started laying she was so intent on her job that it was unnecessary to use a glass cover. The eggs were then transferred singly or in numbers (according to the nature of the experiment) to numbered tubes placed in racks in an unheated room. The *Agabus* eggs were usually kept in 2-inch glass tubes and the *Dytiscus* eggs in larger tubes. The parasites in *Agabus* eggs developed well in corked tubes ; by placing silk round the cork before inserting it small imagines were prevented from creeping into cracks in the cork. As the *Dytiscus* eggs so frequently went bad, the tubes containing them were covered with silk affixed with Sellotape, or the eggs were placed in a covered jar, but even so, eggs in which females had been seen to lay often decomposed.

The imagines used in the many experiments undertaken to try to ascertain the relation of the brachypterous to the normal form were mounted on slides in polyvinyl lactophenol to allow of comparison with their offspring. This medium preserved the wings well but other parts were liable to shrink. Dissections of parasitised host eggs were made in Insect Ringer solution.

V. Observations on the Behaviour of *Caraphractus* with Eggs of Various Aquatic Insects

Other Recorded Hosts

It has been already mentioned (p. 535) that *Caraphractus cinctus* has been recorded erroneously as a parasite of the eggs of dragonflies. Thanks to the kindness of Mr. A. E. Gardner in supplying me with eggs of two species of Odonata, I have been able to watch the behaviour of the females when placed with them. The eggs tested were those of the Dragonfly, *Aeshna grandis* (L.) and the Damsel-fly, *Coenagrion puella* (L.). The leaves containing the eggs of these two species were tested separately with several females of *Caraphractus*. They walked over the leaves with the *Aeshna* eggs, palping them with their antennae, a sure sign that they are looking for eggs. They showed no interest in the scars beside these eggs, but laid readily in eggs of *Ilybius fuliginosus* offered to them. No *Caraphractus* were reared from the *Aeshna* eggs, though they were left with the Mymarids for several days. Just the same results were obtained with the *Coenagrion* eggs, which were equally ignored by the females. Several *Caraphractus* were seen to insert their ovipositor for a few moments into the *Potamogeton* leaf in which the eggs were laid, but not over the places where they were embedded.

Since *Caraphractus cinctus* has been recorded from America from the eggs of *Notonecta* (Matheson and Crosby, 1912), I made many attempts to obtain parasitism of the eggs of *Notonecta glauca* L., but without success. At the end of March, 1957, I confined females of *N. glauca* with plants of *Juncus articulatus* grown indoors, and obtained eggs which were embedded in the rush leaves so as to leave a large area of each egg exposed. The chorion of the egg appears very thick and is studded with extremely minute closely placed spines. The female *Caraphractus* took great interest in these

eggs and punctured them with her ovipositor repeatedly, but usually only for 5–10 seconds. This resembles the behaviour normally accorded to eggs of water beetles that are already parasitised, but there was no possibility that the *Notonecta* eggs, obtained in the laboratory, could have been previously parasitised. When trying to pierce the egg the ovipositor often glanced off its convex exposed portion although it appeared to penetrate at the sides and ends, but it was rarely held steady for more than 5 or 10 seconds, and only once was a female seen to keep her ovipositor in an egg for 2 minutes. Many of the *Notonecta* eggs placed with the Mymarids developed red punctures from the ovipositor holes of *Caraphractus* but not a single *Caraphractus* was reared from any of the many eggs offered, and, though I dissected several *Notonecta* eggs, I could find no eggs or larvae of the parasite. Some of the *Notonecta* eggs exposed to the Mymarids hatched but others died. The *Caraphractus* females used for these experiments were tested with eggs of *Dytiscus* or *Agabus* which they readily parasitised. It appears that, although the *Notonecta* eggs are of much greater interest to *Caraphractus* than the eggs of the Odonata offered, they do not provide a suitable host.

Other Eggs Offered

The eggs of *Haliplus* were very common, embedded in the stems and leaves of *Juncus articulatus* in the pools where I took the Mymarid. They are very small, only 0·59 mm. long, and the females took no interest in them. Large *Corixa* eggs (probably of *C. dentipes* Thoms., as a male of this species was taken nearby) were of interest to the female *Caraphractus*. She was watched several times trying to pierce an egg but each time her ovipositor slid off; however the eggs were left with the female and each showed later a black puncture spot but they died without showing any *Caraphractus* larvae. There is thus no evidence that any of these eggs are suitable for the parasite.

VI. Outline of Life History of *Caraphractus cinctus* Walker

The female oviposits under water in the eggs of various Dytiscidae, laying through the plant tissue when this surrounds the egg, or directly into the egg if it is exposed. Two or three eggs are normally laid in an *Agabus* egg at each oviposition during one thrust of the ovipositor, and the female then seeks another egg. Both newly-laid eggs of *Agabus* and those showing a more advanced development are successfully parasitised. When the host embryo is well developed (showing body bristles, mandibles and dark ocelli) the Mymarid directs her ovipositor deep into the egg so that it penetrates the mid-gut of the embryo and there the parasite larvae develop. I have mostly bred only one or two imagines from such advanced host eggs of *A. bipustulatus*; there is, of course, less food to consume as the chitinous parts of the host larva are left intact. Advanced eggs of *Dytiscus* are rarely parasitised successfully and they are less attractive to the females than newly-laid eggs. The larvae consume the entire contents of a newly-laid *Agabus* egg, and normally that of a *Dytiscus* egg also, provided sufficient larvae are present to cope with so much food.

The *Caraphractus* egg increases greatly in size after laying, showing that the chorion is elastic, as it must be to have passed down the narrow ovipositor—

Fulton (1933) describes the passage of the egg down the ovipositor in *Habrocytus* as " like sand through an hour glass ".

No mandibles have been found in any instar of the larva ; in the growing larva the liquid contents of the egg are sucked in by the small round mouth, and there is a constant rhythmic movement of the oesophagous, apparently brought about by the contraction of the muscles connecting the wall of the fore gut with the dorsal body wall. The young larvae are able to move about within the egg, and can be watched through the transparent shell. I have never seen them attack each other and their soft mouthparts would render them powerless to inflict injury. Indirect evidence supporting this view is shown by the following observations. It frequently happens in *Agabus* eggs that a quite small larva may reach the pupal state while larger specimens in the same egg are still full-grown larvae, showing that a small larva is not crushed and the contents swallowed. Moreover such numbers of larvae may develop in superparasitised eggs of *Dytiscus* that the host egg ruptures and all perish (p. 548). Were the larvae able to feed on each other this would not occur.

Conspicuous white spots are visible over the mid-gut of the larger larvae. They are situated in the mid-gut wall and contain concretions which may be urates. No solid excrement is shed by the larva but the concretions are later discharged in the meconium when the imago has emerged from the host egg (Jackson, 1958*a*). The life cycle in summer takes about a month ; in an incubator at 23° C. it occupies only 18 days. Four generations and a partial fifth have been bred in a cool room in the course of a year, but the generations overlap and breeding occurs from spring till late autumn. The winter is passed in the eggs of *Agabus* and *Ilybius* while the Mymarid is in the prepupal state.

Emergence is effected by the imagines biting a hole with their mandibles in the host shell. The males usually emerge first and mate with the females as they come out of the egg, but mating may also occur out of water. A single mating is sufficient to allow of fertilised (female) eggs being laid, along with male eggs, throughout the life of the female. The female of normal size, given access to host eggs, lives about 10 days ; deprived of host eggs it dies sooner. The males may live 14–15 days. The females are able to start laying within 24 hours of emerging and large females may deposit over 100 eggs. When host eggs are provided the females usually remain continuously under water ; the males more often rest out of water on the sides of the receptacle. Both sexes can fly readily. The imagines have a well developed air-filled tracheal system. No external air supply is carried and respiration under water must be cutaneous.

Arrhenotokous parthenogenesis occurs and unmated females usually lay quite readily, depositing as a rule two or three male eggs at one thrust of the ovipositor, but sometimes they are slow to start laying. The progeny of unmated females usually develop normally, large males being bred from *Agabus* eggs in which only two eggs have been laid and small males, often brachypterous, resulting from superparasitism. Up to 95 males have been reared from one unmated female.

However, very different results were obtained in the case of one particular strain derived from a female (No. 217) reared from an egg of *Ilybius fuliginosus* collected from a Fife pond, for these unmated females were strangely infertile. Fifty-three were placed separately or in batches with 224 *Agabus* eggs, and though

they were observed ovipositing in many of these eggs in the normal fashion, their progeny mostly died at various stages in their development, or else the host eggs died before larvae of the parasite were visible. Instead of rearing over 400 males as I would expect with unmated females of the normal strain, only about a dozen males completed their development. However, when some of the same females were mated, they produced fertile offspring, preponderantly female like their mother, for she produced 84 daughters and one son in 42 eggs of *Agabus bipustulatus* offered singly, quite different from the usual sex ratio in *A. bipustulatus* eggs in which males are more numerous, for in an exactly similar experiment with a female of normal strain using 52 host eggs offered singly, 31 males and 90 females were bred.

Rimsky-Korsakov (1925) states that there is no parthenogenetic development of eggs in *Caraphractus cinctus*, and it is possible that his observations in Russia may have been based on a similar strain.

VII. The Hosts Used

I have reared *Caraphractus cinctus* from collected eggs of *Dytiscus marginalis* (Plate II), *Ilybius fuliginosus*, *I. ater* and *Agabus sturmii* and I have bred it in the eggs of all these species and also of *Colymbetes fuscus*, *Hydroporus planus*, *Agabus bipustulatus*, *A. nebulosus*, *A. labiatus* and *A. chalconatus*.

VIII. Numbers Reared from Host Eggs

Size of Host Eggs and of Caraphractus cinctus

Since the host eggs on which this Mymarid can develop range in size from an egg of *Hydroporus planus* measuring only 0·68 mm. to a *Dytiscus* egg measuring up to 8·2 mm., the numbers of imagines reared in the eggs of different species varies from one to over 60. The size of the imagines of *Caraphractus* is also extremely variable, from a brachypterous female of 0·82 mm. (Plate Ic) with wings of only 0·44 mm., bred from an *Ilybius* (?) egg, to a female of 1·54 mm. with wings of 1·64 mm. (Plate Id) from a *Dytiscus* egg. It is not always the smallest specimens that are found in an *Agabus* egg, for a singleton in an *Agabus* egg is large, while small, and even brachypterous specimens, may occur along with large specimens in an overcrowded *Dytiscus* egg.

Numbers Reared from Agabus *Eggs*

In the accompanying table (p. 550) particulars are given of the numbers of parasites reared from host eggs which were isolated before the imagines emerged. The eggs were exposed to the attack of one or several females sufficiently long to give ample opportunity for superparasitism to occur, and the percentage of specimens obtained with wings short or of intermediate length is indicated (R) below each total bred. Not included in this table are the many eggs, mostly of *A. bipustulatus*, which I isolated after a single attack by one female, *i.e.* when the ovipositor had been inserted once only. Such eggs yielded usually two or three imagines, sometimes only one, and, on rare occasions, four or even five. It is quite clear from observations on discrimination and restraint in laying, that an *Agabus* egg subjected to more than one laying is in most cases superparasitised, and an egg once parasitised is normally rejected by a laying

female, so it is not surprising to find that, in all four host species listed, eggs containing two or three parasites are most common.

The four species of *Agabus* parasitised successfully by *Caraphractus*—*bipustulatus*, *sturmii*, *labiatus* and *nebulosus*—have eggs ranging in size from 1·3–1·5 by 0·68 mm. in the first to 1·0–1·1 by 0·5 mm. in the last. Even this small difference in size has an effect on the number of *Caraphractus* reared and on the proportion showing wing reduction. Brachypterous specimens, especially females, were particularly common in collected eggs, believed to be those of *A. sturmii*, obtained in June and early July, in the hot dry summer of 1955, and the data from these collected eggs are recorded under column 5 of the table, for comparison with the bred specimens. *Agabus chalconatus* is not included in the table as it was not a suitable host, for, though *Caraphractus* laid in the eggs, the few imagines that developed were deformed or had the abdomen distended, and most of the eggs punctured by the Mymarid died, developing fungus.

Numbers Reared from Eggs of Ilybius fuliginosus

It will be seen from the table that more eggs of *fuliginosus* than of *A. bipustulatus* are recorded as having four and five imagines, though the egg of *fuliginosus* is slightly smaller. The proportion of specimens with reduced wings is, however, much the same in the four to six imagines to the egg class in the two species, namely 9·0 per cent. in *fuliginosus* and 8·5 per cent. in *bipustulatus*. The *fuliginosus* eggs were all parasitised within the hollow leaves of *Juncus articulatus*.

Numbers Reared from Eggs of Ilybius ater

From two to nine imagines, very variable in size, have been bred from one egg of this species.

Numbers Reared from Eggs of Colymbetes fuscus

The females laid readily in the eggs of this species but there was a high mortality amongst the progeny, and only from a few eggs were imagines reared, five or six to an egg, none brachypterous.

Numbers Reared from Eggs of Dytiscus marginalis

The number emerging from these eggs is very variable, and there is in many cases a considerable residue of larvae, pupae and imagines which die within the egg after the imagines which emerge first have left. The presence of emergence holes in these large eggs renders conditions unsuitable for the development of the remainder, except for occasional imagines which may emerge a day or two after the others. Residual larvae cannot complete development in an opened *Dytiscus* egg, though this has frequently happened in *Agabus* eggs. I have found *Dytiscus* eggs with emergence holes still containing dying larvae of *Caraphractus* in aquatic plants submerged in pools, so residual larvae are not a result of breeding in captivity.

The most successful parasitism has been obtained by using a single female to lay in one or two *Dytiscus* eggs, and when only 25–35 parasites develop these are vigorous and leave few residual specimens. Fifty-six individuals (eight

males and 48 females) have emerged successfully from a *Dytiscus* egg parasitised by one female, and four female pupae and five larvae were left in the egg. Such an egg is, however, overcrowded, some imagines being small and short winged. If a *Dytiscus* egg contains too few parasites there is, on the other hand, too much food for the larvae to consume and the imagines that develop are very large with distended abdomens, and only one or two may be sufficiently vigorous to emerge. The physogastric specimens die without breeding. As few as ten imagines, two males and eight females, all very large, emerged from one *Dytiscus* egg, leaving only one residual female in the egg. Plate Id is a photograph of a female emerged from a *Dytiscus* egg with only five other imagines, all females, and two male pupae. Salt (1938) observed a similar effect of too much food on individuals of *Trichogramma* bred in a large egg.

IX. Effects of Superparasitism with Observations on Sex Ratio

Superparasitism is deemed to have occurred when so many imagines develop in a host egg that one or more are of unusually small size and often (though not invariably) brachypterous. Superparasitism is usually avoided by the discrimination and restraint exercised by the laying female (p. 534) but it does occur under the following conditions, (1) when several females attack an egg at the same moment, (2) usually when a female that has not laid before encounters a parasitised egg, and (3) when a female has been deprived of the opportunity of laying for a few days.

Effect on Fertility

The small imagines produced by superparasitism live at most for a few days and, though both sexes are fertile, the females lay far fewer eggs than specimens of normal size, although, as is shown in Plate Ia and b, full-sized specimens may be bred from a brachypterous female. The reduced fertility of small females has been observed by other workers, *e.g.* Salt (1940) in *Trichogramma evanescens* Westw., Edwards (1954) in the Pteromalid, *Mormoniella vitripennis* Walker, and Narayanan and Subba Rao (1955) in the Braconid, *Microbracon gelechiae* Ashmead. In *Caraphractus* only a few specimens (very small and feebly sclerotised, with small wings imperfectly expanded) have been observed in my experiments which approach the condition of the runts described by Salt (1940), which he found were produced by superparasitism in *Trichogramma evanescens*.

Effect on Wing Reduction

Superparasitism produces conditions under which wing reduction of varying degrees may occur. It is most common in the eggs of the smaller *Agabus* such as *A. sturmii*, and less common in the larger eggs of *A. bipustulatus* and *I. fuliginosus* from which six small imagines with wings of normal size are often reared. Brachypterous specimens are occasionally bred from uncrowded eggs, as when one small short-winged imago emerges precociously, and only two larvae remain in the egg. They have also been obtained from advanced host eggs and their production is probably due to a lack of food at the time the wing-discs are developing. The brachypterous specimens, though able to use their short

wings for swimming, will be unable to disperse in the air, and if they float to the surface they become entangled in the surface film.

Effect on Mortality

Superparasitism frequently results in the death of all the larvae. *Dytiscus* eggs may become so heavily parasitised that the shell splits longitudinally and the larvae fall out and perish. *Agabus* eggs placed with many females often become opaque and then mouldy before the presence of the larvae can be recognised. Not only may the larvae die within the egg but imagines in crowded eggs often fail to emerge.

Effect on Sex Ratio

An increase in the numbers of males in superparasitised eggs has been observed by many workers on parasitic Hymenoptera. It is usually believed that the male larvae are more viable, or " intrinsically superior " as Salt (1936) suggested for *Trichogramma evanescens*. I have no evidence that this is the case in *Caraphractus* for I have observed that when six larvae, two males and four females, compete within an egg of *A. bipustulatus* for the available food (as the result of simultaneous ovipositions by two females), it is the female larvae which most commonly develop at the expense of their brothers, the males reared being smaller and sometimes brachypterous. Lund (1938) has also found that in superparasitised eggs of *Sitotroga*, the female of *Trichogramma evanescens* is apparently able to thrive at the expense of the male. In a preliminary experiment on mass breeding, using many females along with males with about 40 eggs of *Agabus sturmii*, a high proportion of males resulted (51·6 per cent.) but six of the 20 female parents used had emerged without males, and may have laid while still unmated. In an exact repetition of this experiment but using only females which had been with males since emergence, the male emergents were 37·7 per cent. Two similar experiments (but with ten females each) were conducted with eggs of *bipustulatus* ; there was a high mortality amongst the eggs and the proportion of male emergents varied from 35·5 per cent. to 38·9 per cent.

When single mated females were confined with several eggs of *Agabus sturmii* and *A. bipustulatus* in small numbers for long enough to allow of repeated ovipositions and the eggs subsequently isolated, there was scarcely any superparasitism (only three *sturmii* eggs with four imagines) and, of the 129 imagines reared from 91 eggs, only 33 per cent. were males. When many *Agabus* eggs are offered to single females the sex ratio again alters to produce more females, as is shown by the following experiments with *A. bipustulatus*.

Experiment	Eggs offered	Eggs parasitised	Numbers reared (♂)	Numbers reared (♀)	Total emerged	Male emergents per 100
1 .	22	22	19	41	60	31·6
2 .	40	30	20	64	84	23·8
3 .	36	27	13	49	62	20·9

An explanation of this varying sex ratio is afforded by observations on individual layings by single, mated, females on eggs of *A. bipustulatus* which were each

placed in a numbered tube directly the female had laid, and the progeny reared. In a series of experiments, to be described in detail in a later paper, the sex ratio was usually found to vary according to the rate of laying. Thus when a single egg is offered to a female at intervals of three hours or more, she usually lays at a single thrust of the ovipositor one male and two female eggs, so that I have been able to obtain an almost unbroken succession of three eggs of these sexes from the same female for several days. If, however, host eggs are supplied to the same female in rapid succession, the number of eggs at each thrust is reduced to two or to one and a much higher proportion of female eggs is laid. Thus, 19 female eggs and only one male were laid by one female in less than an hour in 11 host eggs offered one after another, while during the five preceding days, when the female was restricted to three eggs a day offered at long intervals, the male sex ratio was much higher, 17 males and 32 females emerging from 18 host eggs. It is thought that when a female lays in one *Agabus* egg directly after another the flow of spermatozoa will be stimulated, so that a higher proportion of the eggs passing into the ovipositor will have been fertilised, and the fact that, in rapid laying, the eggs pass in pairs or singly, instead of in the usual threes, may be of significance in facilitating their fertilisation. This is contrary to the view expressed by Flanders (1939) that an increase in the rate of oviposition probably increases the number of eggs escaping fertilisation, but this suggestion does not appear to rest on experimental evidence.

In numerous experiments, I have found that a single mated *Caraphractus* female produces a higher proportion of female offspring in a *Dysticus* egg than when confined with several *Agabus* eggs. Thus 38 *Dytiscus* eggs were each exposed to a single mated female and it was possible to distinguish the sex of 881 of the offspring, and there were only 17·2 per cent. males. In those 38 eggs the residue of larvae (or of pupae too decomposed to sex) was small, totalling about 100, and, in all those eggs in which few or no residual larvae were left, the proportion of females was high. This change of sex ratio in large as compared with small host eggs is borne out by observations on collected eggs of *Dytiscus* and of *Agabus sturmii*, the data on the latter species being recorded in column 5 of Table I. This difference of sex ratio in large as compared to small host eggs is readily explained by rapid laying, for on encountering an unparasitised *Dytiscus* egg, the female lays steadily until a sufficiency of eggs has been deposited. This method of sex regulation enhances the likelihood of all the females mating, since when eggs of *Agabus* are scarce and only found after long intervals of searching, a male develops in most eggs along with two females, but when *Agabus* eggs are close together, or a large egg like that of *Dytiscus* is encountered, fewer males will suffice to mate with all the females, as one male has been found capable of mating successfully eight times. Other workers, notably Shevirev (1913) and Brunson (1937) (discussed by Flanders (1939)), have observed that females predominate in large hosts and they believe that the mated female is able to regulate the sex of her offspring, so as to lay more female eggs in the larger " preferred " hosts. It would be interesting to know whether the factor of rapidity of laying has any bearing on the cases dealt with by these writers.

When a *Dytiscus* egg is exposed to the attack of many females (all having been with males and therefore probably mated) it may become packed with larvae; there is usually a high mortality and the sex ratio changes, as in *Agabus* eggs, to produce many more males. In one case where a *Dytiscus* egg was exposed

TABLE I.—*Showing numbers and sexes of* Caraphractus cinctus *bred from eggs of four species of* Agabus *and from* Ilybius fuliginosus.

No. of imagines to host eggs	(1) *Agabus bipustulatus*			(2) *Agabus sturmii*			(3) *Agabus labiatus*			(4) *Agabus nebulosus*			(5) Collected *Agabus* eggs, probably *A. sturmii*			(6) *Ilybius fuliginosus*			Total eggs	Total ♂	Total ♀	Total imagines
	No. of eggs	♂	♀	No. of eggs	♂	♀	No. of eggs	♂	♀	No. of eggs	♂	♀	No. of eggs	♂	♀	No. of eggs	♂	♀				
One imago	5	.	5	3	.	3	.	.	.	1	.	1	3	.	3	1	.	1	13	.	13	13
Two imagines	15	13	17	45	32	58	3	2	4	3	4	2 (16·6% R.)	18	14	22	.	.	.	84	65	103	168
Three imagines	11	11	22	24	28	44 (1·3% R.)	3	4	5	10	12	18 (13·3% R.)	15	24	21	11	9	24	74	88	134	222
Four imagines	6	9 (16% R.)	15	11	17	27 (13·6% R.)	3	6	6 (50% R.)	1	2	2 (75% R.)	3	7	5 (66% R.)	12	13	35	36	54	90	144
Five imagines	9	18	27 (6·8% R.)	3	11	4 (46% R.)	1	3	2 (20% R.)	.	.	.	5	5	20 (84% R.)	10	12	38 (14% R.)	28	49	91	140
Six imagines	4	11	13 (4·1% R.)	.	.	.	.	.	.	.	.	.	2	11	1 (83·3% R.)	4	7	17 (16%	10	29	31	60
Seven imagines	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	4 (14·2% R.)	1	3	4	7
Totals	50 Eggs	62 ♂	99 ♀	86 Eggs	88 ♂	136 ♀	10 Eggs	15 ♂	17 ♀	15 Eggs	18 ♂	23 ♀	46 Eggs	61 ♂	72 ♀	39 Eggs	44 ♂	119 ♀	246 Eggs	288 ♂	466 ♀	754 Total

Note.—R indicates the proportion of specimens with reduced wings (of intermediate length or short) expressed as a percentage of the emergents in each group. The purpose of the experiments was to find out if brachypterous specimens developed in superparasitism; hence quite a number of host eggs containing two to three parasites were not isolated and are not included in the tables. The progeny of females known to be unmated is excluded.

to ten females, all the 67 offspring reached the adult stage and there were 26 males and 41 females, but usually a large number of larvae fail to develop. The change in the sex ratio is not due to overcrowding alone or to one sex being less viable than the other, for, as noted on p. 546, a single female laying undisturbed in a *Dytiscus* egg produced 52 females, only eight males and five residual larvae, while in an egg first parasitised by an unmated female and then placed with a mated female, 42 males and only five females and one pupa and seven larvae resulted.

I think that when eggs are exposed to the attack of many females the normal laying habits of the female are interrupted so that more male eggs are deposited. Perhaps also the female, so quick to recognise an already parasitised egg as unsuitable, may not receive through her ovipositor, in its preliminary probe into such an egg, the stimulus required for fertilising the usual proportion of her eggs, so that more male eggs are laid, while in an unparasitised or " preferred" host more female eggs are deposited. There seems no doubt from my experiments that the production of fertilised eggs is stimulated by the rapid finding of suitable hosts or of a single large host.

It has thus been shown that the sex ratio in *Caraphractus* is highly variable, depending largely on the number and size of the eggs supplied to the laying female and on whether the female is laying alone or along with others. It is further complicated by the fact that a strain has been discovered, bred from a single female (No. 217), which produced almost entirely female eggs in *Agabus* eggs and whose daughters, when unmated, rarely produced healthy males (p. 544). Professor P. W. Whiting, whom I have consulted in regard to this abnormal strain, informs me that " the problem of sex determination is fundamental to sex ratio and this is not as yet explained for the chalcidoids ".

It has often been observed that in cultures of Hymenopterous parasites during several generations, the proportion of females bred decreases, even to an extent where only males are produced and the stock dies out. Simmonds (1947) found that in breeding *Anoplex carpocapsae* (Cush.) for use in biological control, a higher percentage of females was obtained by breeding from males and females selected from " high sex-ratio families " and he suggests that the sex ratio in this case is genetically determined. He notes that on bringing field material into the laboratory, the sex ratio drops considerably in the first bred generation and states that the cause of this initial drop is obscure. From my observations on *Caraphractus* it has been found that an increase of males results as a consequence of confining too many parasites with too few hosts, but if a single mated female is confined with plenty of hosts, the proportion of females bred is high. It seems a possibility that under artificial breeding conditions too many parasites may be used and this may account for increasing numbers of males being bred.

In conclusion from the evidence given on superparasitism it is clearly of great importance to the survival of the species that the female should lay just the right numbers of eggs, not too many or too few, in hosts of varying size, so that strong and fertile imagines are produced. The female *Caraphractus* gauges this problem, on the whole, very well owing to her remarkable powers of discrimination and restraint in laying. These powers are perfected to a high degree and are applied not only to the eggs of the smaller water beetles but also to that of *Dytiscus*, which a female will reject if it has been parasitised a few

hours previously. When restraint breaks down through lack of hosts or the presence of too many parasites, superparasitism occurs.

X. Summary

An account is given of the methods employed to obtain eggs of various Dytiscidae laid under conditions excluding the possibility of previous parasitism and therefore suitable for the experimental breeding of the Mymarid, *Caraphractus cinctus* Walker.

This parasitoid can develop successfully in eggs of greatly varying size, since it parasitises the eggs of both large and smaller Dytiscidae. In the eggs of *Agabus* two to three individuals normally develop, but up to six small imagines may emerge from a superparasitised egg of *A. bipustulatus* L.

In an egg of *Dytiscus marginalis* L., 25–35 *Caraphractus* imagines may develop, of large size and vigorous. Over 50 imagines have sometimes been reared from one egg but some of these are small. Overcrowded eggs may burst so that the larvae and pupae fall out and perish.

An outline is given of the life history of *Caraphractus cinctus*. The larvae have no apparent mandibles and appear unable to injure each other. The imagines emerge from the egg by biting a hole in the shell with their mandibles ; they live from 10 to 15 days and have never been seen to take food.

The large females are very fertile and may deposit over 100 eggs. The female shows marked discrimination and restraint in laying and this largely prevents superparasitism.

Superparasitism leads to the production of very small specimens, often with short wings. Brachypterous females are short lived and less fertile than normal females, but they can produce offspring of full size.

The effects of superparastism on sex ratio are discussed. In mass breeding experiments there is an increase in the proportion of males reared, but when a single mated female lays alone in *Agabus* eggs provided in quick succession, or in a single *Dytiscus* egg, a high proportion of females results.

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Caraphractus cinctus Walker

A.—Brachypterous female bred in an egg of *Agabus sturmii* Gyll. (along with two other females and one male) from macropterous parents. Mounted in polyvinyl lactophenol.

B.—Macropterous daughter of female in figure A bred in an egg of *Dytiscus marginalis* L. with nine other females, three males and several larvae.

C.—Brachypterous female bred with five others and one male from an egg, probably of *Ilybius fuliginosus* F., collected in *Juncus articulatus* L., at Gilston, Fife, 9.vi.54. Euparal.

D.—Large female bred with only five others and two male pupae from an egg of *Dytiscus marginalis*, from a female and male of normal size bred from an egg of *A. sturmii*. Polyvinyl lactophenol.

(All figures at same magnification.)

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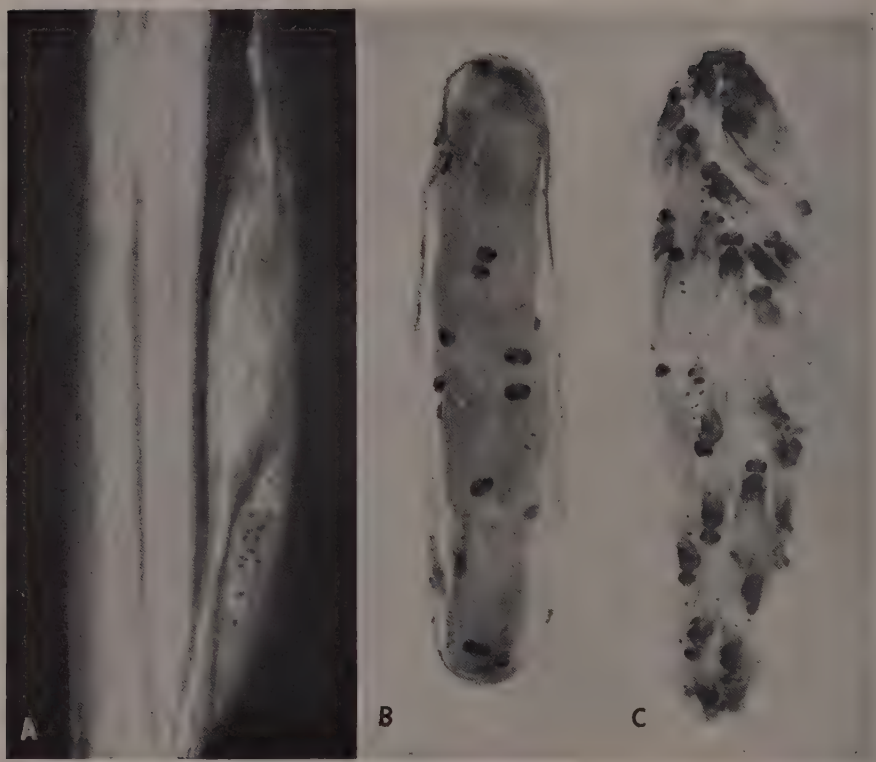

A.—Two eggs of *Dytiscus marginalis* laid in sheathing leaf of *Juncus articulatus*. Both eggs were parasitised by *C. cinctus* About × 6½.

B and C.—Pupae in two eggs of *D. marginalis*, collected at Gilston, Fife, in glycerine jelly. In figure B the pupae are younger, with only head and eyes distinguishable in the photograph. There are fewer pupae in this host egg and they are therefore larger. The dark dots, most distinct in figure C, are oviposition punctures. × 12.

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ERRATUM.

p. 226, line 39, after " 1955–56 " insert " was also mild but was followed by a short cold spring. Winter 1956–57 . . . "